Protected area evaluation for the conservation of endangered Amazon river dolphins (*Inia geoffrensis*)

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A B S T R A C T

The potential value of protected areas for the conservation of cetaceans is widely recognized; however, few evaluation methods exist to assess their effectiveness. In this study, a modeling approach based on long-term mark-recapture/resight data was used to assess the effectiveness of a Brazilian reserve in protecting endangered Amazon River dolphins or boto (*Inia geoffrensis*), a species killed for use as fish bait. We built an annual discrete-time model with subdivisions based on hydrological periods and age classes. It included transition probabilities in and out of the reserve that were estimated utilizing multi-state mark-recapture models. To evaluate five reserve configurations, we re-estimated the transition probabilities to represent changes in the reserve boundaries. Model predictions showed that four scenarios, including one representing the existing boundaries, would be insufficient to protect the local boto population ($n_o = 528$) and a steep decline in abundance would occur in the next 50 years ($0 \leq n_{50} \leq 108$). However, one reserve configuration, encompassing both flooded forests and adjacent river habitats, and including beaches and channel/floodplain entrances, resulted in a nearly stable population in the same time frame ($n_{50} = 515$). These findings suggest that, with careful design and efficient management, protected areas could be an effective conservation tool for boto populations that exhibit site fidelity to Amazonian floodplains. With appropriate mark-recapture/resight data, the modeling framework employed could be extended to evaluate and design protected areas for populations of other species in other systems.

1. Introduction

Protected Areas (PAs) are recognized as a potentially valuable tool for the conservation of aquatic mammals (Hooker et al., 1999; Reeves and Reijnders 2002, Hooker and Gerber, 2004; Kreb and Budiono, 2005; Hoyt, 2005; Portocarrero Aya et al., 2010; Gormley et al., 2012). Potential benefits of PAs for cetaceans include protection of feeding, nursery, and rest areas (Hoyt, 2005; Notarbartolo-Di-Sciara et al., 2008), as well as protection from incidental mortality in fisheries (Read, 2008) and deliberate killing (Robards and Reeves, 2011; Mintzer et al., 2015, 2018). Although numerous PAs have been established throughout the world with the purpose of protecting aquatic mammals (Hoyt, 2005),

few assessments have been conducted to determine the effectiveness of these PAs in protecting the target species.

To our knowledge, only one set of studies has systematically quantified the effectiveness of a PA in decreasing mortality of a cetacean population. Using population viability analysis, Slooten et al. (2006) concluded that the Banks Peninsula Marine Mammal Sanctuary in New Zealand was insufficiently large to effectively protect the local population of Hector's dolphins threated by incidental entanglement in gillnets. Subsequently, Slooten (2007) compared four possible PA scenarios for Hector's dolphins and identified two potential PA scenarios that could significantly reduce population decline. Later, Gormley et al. (2012) estimated survival rates of Hector dolphin's for pre-sanctuary

and post-sanctuary periods and concluded that survival rates had improved since inception of the sanctuary, albeit not enough to allow population recovery. This last study provided the first empirical evidence that PAs can be effective in decreasing cetacean mortality.

With growing efforts to establish PAs for cetaceans (e.g., Trujillo et al., 2010), it is important to continue to develop PA evaluation methods. The functional extinction of the Baiji or Yangtze River Dolphin (*Lipotes vexillifer*) (Turvey et al., 2007) and the critical status of the vaquita (*Phocoena sinus*) (Aragon-Noriega et al., 2010; Jaramillo-Legorreta et al., 2017) emphasize the importance of developing evaluation techniques and effective protection mechanisms. PAs set up for the purpose of protecting these two species have failed primarily due to insufficient enforcement, lack of local participation and acceptance, or because they were implemented too late (Turvey et al., 2007; Aragon-Noriega et al., 2010). An urgent need exists to evaluate the effectiveness of PAs in protecting cetaceans to ensure PA initiatives meet their potential and are not creating false impressions of conservation.

In South America, deliberate killing for use as bait has become an important threat affecting the endangered Amazon River dolphin or boto (*Inia geoffrensis*) (da Silva et al., 2018a). Since the mid-1990s, boto carcasses have been used to attract the catfish *Calophysus macropterus* commonly known as *piracatinga* or *mota* (Gómez et al., 2008; Loch et al., 2009; Trujillo et al., 2010; da Silva et al., 2011; Gómez-Salazar et al., 2012; Iriarte and Marmontel, 2013a, 2013b; Brum et al., 2015; Mintzer et al., 2018). An international market has developed involving the catch of *piracatinga* in several Amazonian nations and the export of this fish to cities in Colombia and Brazil (Trujillo et al., 2010; da Silva et al., 2011).

Where relevant long-term data are available, the level of targeted killing has caused depletion of the boto population (da Silva et al., 2011; Mintzer et al., 2013; da Silva et al., 2018b).

Spatial protection has been suggested as a conservation tool for botos (e.g. Portocarrero Aya et al., 2010; Trujillo et al., 2010; Mintzer et al., 2018). Although, to date, there have been no PAs specifically created for the boto (Portocarrero Aya et al., 2010), populations occur in PAs throughout their range (e.g., Aguaro-Guariquito National Park in Venezuela, Pacaya-Samiria National Reserve in Peru, Cuyabeno Wildlife Production Reserve in Ecuador, Rio Pure National Natural Park in Colombia, and the Mamirauá Sustainable Development Reserve in Brazil; McGuire and Winemiller, 1998; da Silva and Martin, 2000; Portocarrero Aya et al., 2010; Utreras et al., 2010). Portocarrero Aya et al. (2010) provide an overview of over thirty PAs in South America with potential to contribute to boto conservation because they include river dolphin habitat. These PAs vary widely in terms of their landscape and management schemes, ranging from strict nature reserves to those including sustainable human use (i.e., International Union for Conservation of Nature (IUCN) Categories I through VI).

Currently, there is limited evidence on the utility of these PAs in conserving botos, and how they could be improved and managed for this purpose (Mintzer et al., 2016). To address these knowledge gaps, we developed a model to assess the effectiveness of various PA scenarios in protecting botos. We utilized the Mamirauá Sustainable Development Reserve (MSDR) in the Brazilian Amazon as a case study to build an evaluative framework. Herein, we describe the steps conducted to develop the evaluation model, explain key parameters, present the
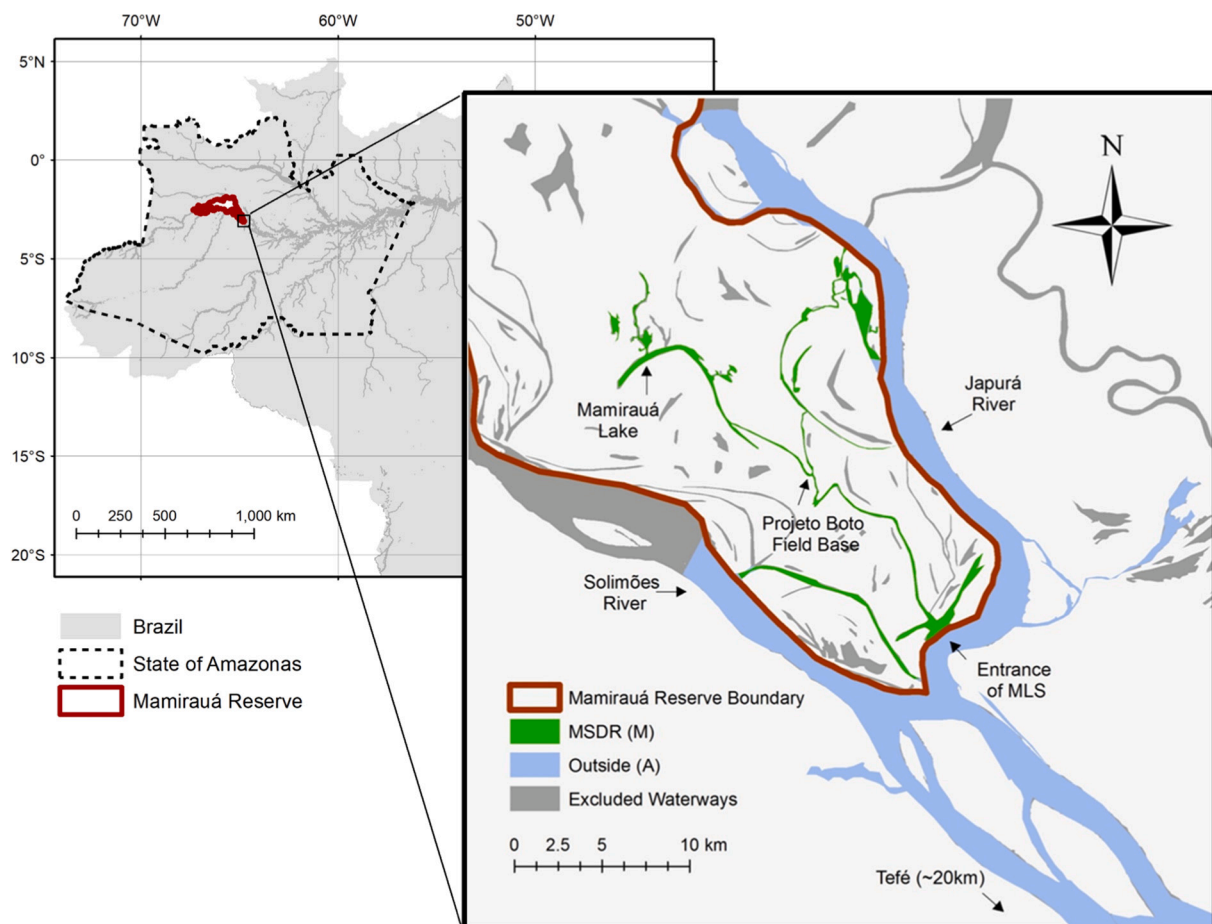

Fig. 1. Map of study site, the southern segment of the Mamirauá Sustainable Development Reserve (MSDR) and surrounding areas, located at the confluence of the Japurá and Solimões rivers in Amazonas State, Brazil. Map displays the two states/locations used in the multi-state models: the MSDR channels and lakes (M), and outside the MSDR (A). The M state/location encompasses the Mamirauá Lake System (MLS). (Modified with author permission: Fig. 1, Mintzer et al., 2016. GIS layers: IUCN and UNEP 2010, DCW and GADM downloaded from http://www.diva-gis.org).

model predictions, and discuss potential improvements in PA design for the conservation of botos.

2. Methods

2.1. Case study

This study took place in and around the southern segment of the Mamirauá Sustainable Development Reserve (MSDR) located at the confluence of the Solimões and Japurá rivers in Amazonas State, Brazil (Fig. 1). The MSDR consists of a focal area of about 260,000 ha and a subsidiary area of approximately 864,000 ha (SCM, 1996). It was originally established in 1990 as an Ecological Station (IUCN Category Ia) and then reestablished in 1996 as the first sustainable use reserve in Brazil (IUCN Category VI) with the goal of enhancing biodiversity conservation with the active participation of local human populations (SCM, 1996). The data used in this study were collected through a research program that has been active in the focal area of the MSDR since 1994, in a subarea referred to as the Mamirauá Lake System (MLS) and adjacent waterways (Fig. 1). The MLS has greater enforcement and researcher presence than other segments of the MSDR (SCM, 1996).

The MSDR is a whitewater floodplain or *várzea*, with aquatic fauna that vary seasonally coincident with extreme water fluctuations (Junk and Piedade, 2005). As the water level rises, the lowland forest floods, channels widen, and lakes form. Although the exact timing of peak high and low water levels varies annually, typically the highest water mark is reached in June, and lowest water levels occur between September and November (Ramalho et al., 2009; IDSM, 2012). Based on the water fluctuations, four main seasonal hydrological periods are recognized in the study area: rising water (RW), high water (HW), falling water (FW), and low water (LW).

Capture-recapture and marking of botos occurred approximately three weeks each year during LW. During capture, botos were freeze-branded with a unique code to allow for subsequent identification. In addition to the capture-recapture events, year-round observational work was conducted throughout the MLS and surrounding areas, including segments of the main rivers. When a boto or group was sighted, the unique codes of any marked individuals were recorded, along with the location. Further descriptions of the field research methods are available in da Silva and Martin (2000), Martin and da Silva (2004a, 2004b), Mintzer et al. (2013), and Mintzer et al. (2016). This work was conducted with approval from the Instituto Chico Mendes de Conservação da Biodiversidade (Sistema de Autorização e Informação em Biodiversidade #13462-1).

As expected from the temporal dynamics of the floodplain, boto distribution in MSDR is highly dependent on water levels (Martin and da Silva, 2004a; Mintzer et al., 2016). During the dry period, botos are concentrated in the main rivers and channels, whereas during the flooded period they enter the MLS (Martin and da Silva, 2004a; Mintzer et al., 2016). A "resident" population of botos occurs in the study area, defined as comprising individuals that are observed there in at least seven of 12 months of the year (Martin and da Silva, 2004b). Because of water level fluctuations, no boto spends its entire life within the MLS; however, some individuals stay near the floodplain system until the water rises enough to allow them back into the MLS (Martin and da Silva, 2004a; Mintzer et al., 2016).

Among PA's that have potential to contribute to boto conservation, the MSDR was a good candidate for evaluation because it consists of *várzea*, which is essential habitat for the species (Martin and da Silva,

2004a; Mintzer et al., 2016; Utreras et al., 2010), and the resident population of botos has been studied for over two decades (Martin and da Silva, 2004b). Although the MSDR was not created with the specific goal of protecting botos, aquatic mammals were considered fauna of interest and included in research and monitoring from the onset of the reserve (SCM, 1996, Pg. 16). River dolphin "distribution, abundance, movement, and social structure" were among environmental studies carried out to inform the MSDR management plan (SCM, 1996, Pg. 51). Currently, the reserve enhances outreach and enforcement, particularly in the MLS study site, that can minimize intentional killing of dolphins for use as bait (Mintzer et al., 2015). Accordingly, the purpose herein was to assess whether the reserve in its current spatial configuration contributes to maintaining boto abundance, and whether expansion of the reserve would enhance this function.

2.2. Model structure

We developed an annual discrete-time model with four subdivisions based on seasonal hydrological periods and seven age classes (Fig. 2). It included transitions into and out of the PA (Fig. 2) that were estimated from the recapture/resighting data. To explore various PA configurations, we re-estimated the transition probabilities to represent a change in the PA boundaries.

The model simulated population abundance for a period of 50 years and predicted population changes from one year to the next for seven age classes. Age classes 1–3 included calves still dependent on their mother. Botos in age classes 4–6 were considered immature, or individuals no longer dependent on their mother, but not yet sexually mature. The final age class 7 consisted of females and males of reproductive age. These age classes were based on previous work suggesting that female botos reach sexual maturity after 7 years of age (Martin and da Silva, 2018).

Because of the importance of water level fluctuations on boto movement and reproduction (Martin and da Silva, 2004a, 2004b; McGuire and Aliaga-Rossel, 2010; Mintzer et al., 2016), the water-level based seasons were incorporated in the model: FW, LW, RW, and HW. Although the exact timing and duration of these hydroperiods vary from year to year, a total duration, in months, was assigned to each period based on water level records from the MSDR during a full decade (Ramalho et al., 2009; IDSM, 2012). Births were represented once a year, at falling water (FW, July–September), since most births occur during this time period (Martin and da Silva, 2018). We used the following equations to estimate changes in abundance from HW to FW (from one year to the next) inside the MSDR:

$$n_{1,t+1} = (B p n_{7,t}) * (\phi^{M\,\hat{}}(1/12))^{L_{HW}}$$

$$n_{2,t+1} = \left(n_1{}^{M} * \left(1 - \Psi_{MCI,HW}^{MA}\right) + \left(n_{1,t}{}^{A} * \Psi_{MCI,HW}^{AM}\right)\right) * (\phi^{M\,\hat{}}(1/12))^{L_{HW}}$$

$$n_{3,t+1} = \left(n_{2,t}{}^{M} * \left(1 - \Psi_{MCI,HW}^{MA}\right) + \left(n_{2,t}{}^{A} * \Psi_{MCI,HW}^{AM}\right)\right) * (\phi^{M\,\hat{}}(1/12))^{L_{HW}}$$

$$n_{4,t+1} = \left(n_{3,t}{}^{M} * \left(1 - \Psi_{MCI,HW}^{MA}\right) + \left(n_{3,t}{}^{A} * \Psi_{MCI,HW}^{AM}\right)\right) * (\phi^{M\,\hat{}}(1/12))^{L_{HW}}$$

$$n_{5,t+1} = \left(n_{4,t}{}^{M} * \left(1 - \Psi_{MCI,HW}^{MA}\right) + \left(n_{4,t}{}^{A} * \Psi_{MCI,HW}^{AM}\right)\right) * (\phi^{M\,\hat{}}(1/12))^{L_{HW}}$$

$$n_{6,t+1} = \left(n_{5,t}{}^{M} * \left(1 - \Psi_{MCI,HW}^{MA}\right) + \left(n_{5,t}{}^{A} * \Psi_{MCI,HW}^{AM}\right)\right) * (\phi^{M\,\hat{}}(1/12))^{L_{HW}}$$

$$n_{7,t+1} = \left(\left(n_{7,t}{}^{M} + n_{6,t}{}^{M}\right) * \left(1 - \Psi_{AdultsI,HW}^{MA}\right) + \left(n_{7,t}{}^{A} + n_{6,t}{}^{A}\right) * \Psi_{Adults,HW}^{AM}\right) * (\phi^{M\,\hat{}}(1/12))^{L_{HW}}$$
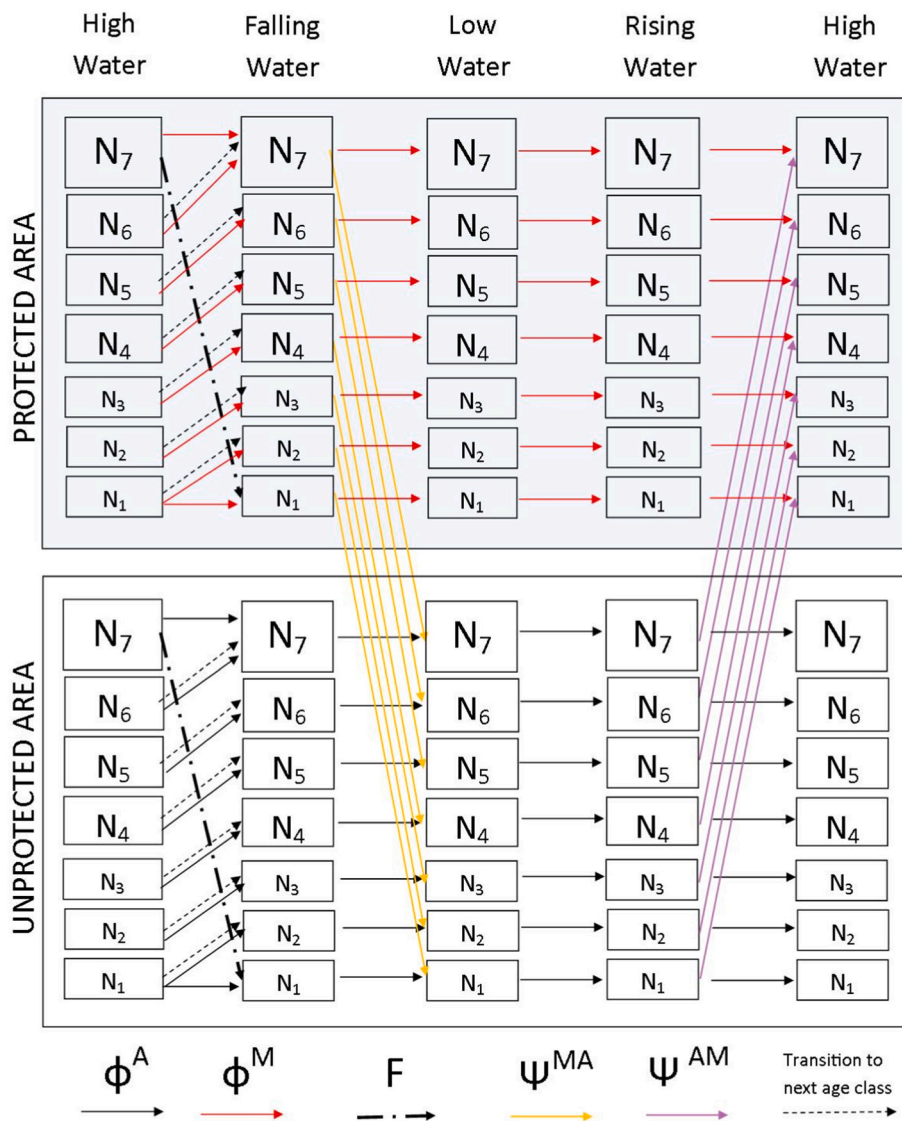
Fig. 2. A schematic representation of the evaluative model showing demographic parameters of botos within the MSDR (top panel) and outside the MSDR (bottom panel) for seven age classes. Apparent survival inside (M) and outside (A) the MSDR is denoted by ϕ^M and ϕ^A respectively. Movement in and out of the MSDR is represented by transition probabilities Ψ^{AM} and Ψ^{MA}. Fecundity is indicated by F. This conceptual model does not display movement throughout all seasons, only at falling and rising water.

where, B = annual fecundity, p = proportion of adult females, ϕ^M = annual apparent survival in the MSDR, ϕ^A = annual apparent survival outside the MSDR, L_{HW} = number of months in HW season, $\Psi^{MA}_{G,\,HW}$ = group (G) dependent seasonal transition probability from inside(M) to outside(A) the MSDR, $\Psi^{AM}_{G,\,HW}$ = group (G) dependent seasonal transition probability from outside(A) to inside(M) the MSDR.

2.3. Parameter estimation

2.3.1. Apparent survival (ϕ)

Apparent survival (ϕ = true survival x (1 - probability of permanent emigration)) estimates of the study population were determined using mark recapture/resight modeling described by Mintzer et al. (2013). In the aforementioned analysis, apparent survival estimates for pre-harvest (1994–2000) and harvest periods (2000−2011) were estimated to be 0.968 and 0.899, respectively. Because no substantial killing of botos occurs inside the MSDR section included in this study (Mintzer et al., 2015), the pre-harvest survival estimate of 0.968 was used as the MSDR apparent survival probability (ϕ^M). A value of 0.834 was assigned as the apparent survival probability (ϕ^A) outside the MSDR. This value was determined using a one-year simulation that accounted for the

proportion of botos inside and outside the reserve during the four hydroperiods. The inside survival was fixed at 0.968 and the outside survival rate was varied until the predicted apparent annual survival was calculated to be 0.899 (the survival rate of the harvest period in Mintzer et al., 2013). Assumptions in the simulation regarding boto proportions and movement were based on Mintzer et al. (2016).

2.3.2. Annual birth rate (B)

The annual birth rate (B) is defined as "the proportion of mature, reproductively active females that give birth in a year, on average." (Martin and da Silva, 2018). The rate was previously calculated as 0.219 for 71 reproductive females from this population (Martin and da Silva, 2018).

2.3.3. Initial abundance (N_0) per age class and proportion of females (p)

The initial abundance was set at 528, which corresponds to the population included in the apparent survival analysis in Mintzer et al. (2013). The initial proportion of botos in each class was determined based on the botos in each age class sighted in 2009 (Mintzer et al., 2013). Proportion of females was 0.485 (Mintzer et al., 2013).

2.3.4. Transition probabilities (Ψ)

Multi-state mark-recapture models in Program MARK (White and

Burnham, 1999) were used to estimate transition probabilities of botos moving from inside to outside the MSDR (Ψ^{MA}), and from outside to inside the MSDR (Ψ^{AM}). We created encounter histories, based on monthly time intervals, for 305 botos sighted between January 2009 and December 2010 (corresponds to Mintzer et al., 2016). For multi-state models, encounter histories represent both the encounter (or sighting) and the state (or location) of the encounter. In our modeling, two states (locations) were defined: inside the MSDR (M) and outside the MSDR (A). If an animal was seen within the MSDR during a month, it was assigned an M for that month. If it was sighted outside the MSDR during a month, it was assigned an A. For instance, an encounter history of M0A describes an individual that was sighted in the MSDR in period 1, not detected in period 2, and seen outside the MSDR in period 3.

Transition probability estimates were calculated across the two states (locations) (Ψ^{MA} and Ψ^{AM}) for each of the four hydrological periods (HW, FW, LW, RW). Program MARK estimates the following three parameters for multi-state recaptures only models: S_t^r = the probability that a boto in location r at time t survives until time $t + 1$, P_t^r = the

probability that a boto is sighted at time t in location r, given that the boto is alive and in the study area at time t, Ψ_t^{rs} = the probability that a boto in location r at time t is in location s at time $t + 1$, given that the boto survived from time t to $t + 1$. S was considered to be apparent survival (ϕ) as defined above. ϕ, p, and Ψ were treated based on *a priori* assumptions and ϕ^M and ϕ^A were fixed at 0.968, and 0.830, respectively (Mintzer et al., 2013). To allow for changes in observation effort through time and across space, p was defined as fully time-dependent (t) and state/location dependent (L). We built models that allowed estimation of transition probabilities (Ψ) for each season of each year and others that restricted estimation of transition probabilities per season across all years. In addition, models were built that allowed Ψ to vary according to sex and age group (G). Four groups were considered: adult males (AM), adult females (AF), mother/calf pairs (MCP), and immature individuals (IMM). Transition probabilities were allowed to vary with all four groups (AM, AF, MCP, and IMM), three groups (adults, MCP, and IMM), or two groups (adults and MCI, where MCP and IMM were combined).

A median $\hat{c}$ goodness-of-fit test on the global model was conducted to
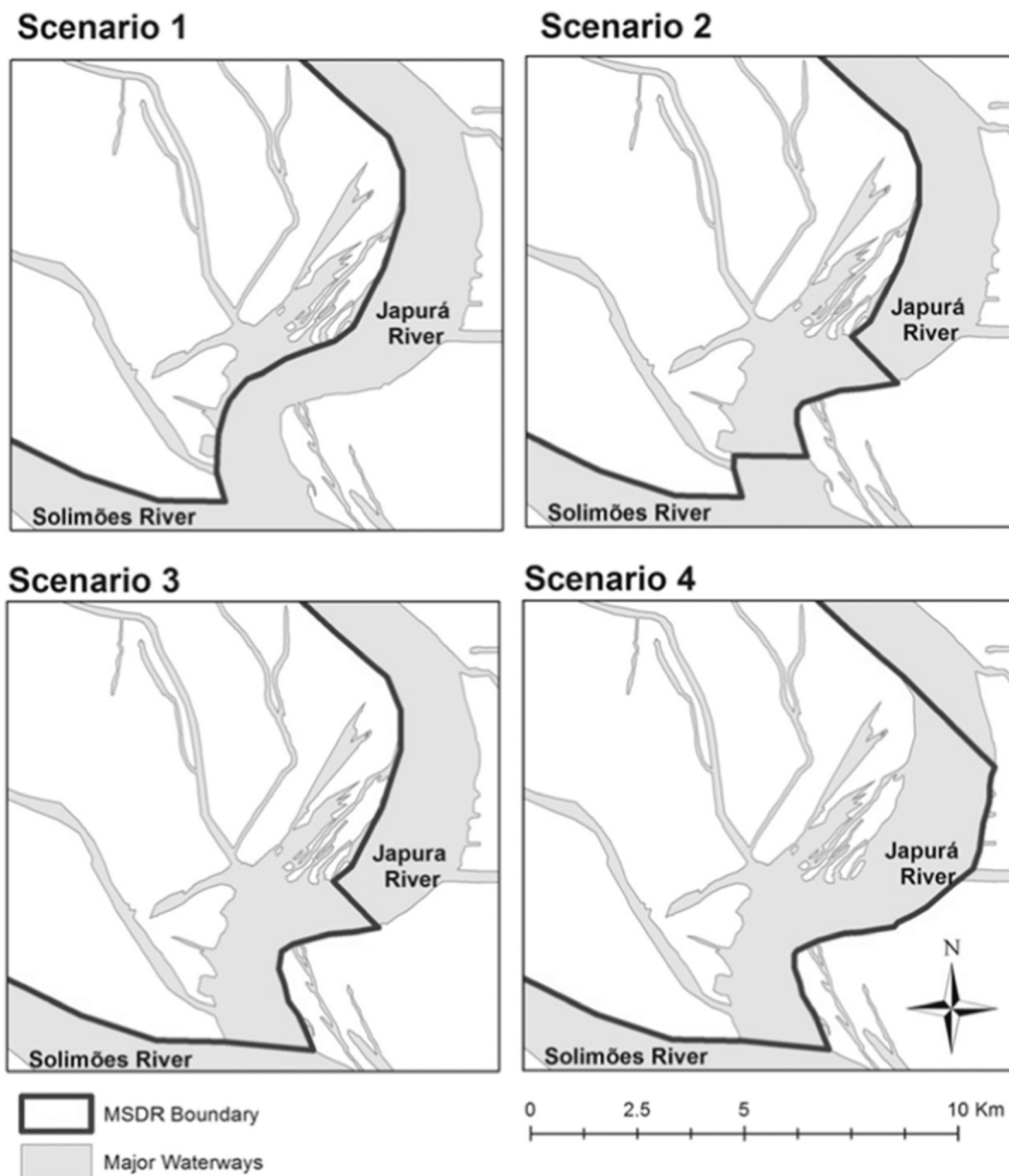

Fig. 3. Protected area boundary scenarios applied in the evaluative model. Scenario 1 represents the true or existing protected area boundary of the Mamirauá Sustainable Development Reserve. Scenarios 2–4 convey situations where the protected area boundary was expanded in the model.

assess overdispersion (White and Burnham, 1999). Akaike's Information Criterion (AIC) was used for model ranking (Akaike, 1973); however, because we applied the estimated c (variance inflation factor) to the model set, we used the small-sample, c corrected version of AIC, QAICc. Additional modeling details are available in the Appendix.

2.4. Scenario building

We built the base model to represent the current PA scenario, with the above parameter estimates, and we checked model performance by comparing the resulting abundance trend to a reported annual decrease in the population of 6.7% (da Silva et al., 2018b). This decrease was calculated independently using standardized count surveys along a 30 km route in the MLS (Fig. 1; da Silva et al., 2018b). The transition probabilities were adjusted to simulate the various PA scenarios that were input into the evaluative model. For these adjustments, we manipulated the input files used in the multi-state models in Program MARK. For example, an original encounter history of AM0A0AAA described an individual that was most often seen outside the MSDR boundaries (in A). If a scenario was being modeled where the MSDR boundaries were expanded, the sightings that occurred in A would be changed to M if they occurred in an area considered newly protected for the scenario. The adjusted encounter history could, for example, result in MM0A0MMM. With each scenario, all capture histories were altered in this manner to represent the areas considered to be newly protected under the scenario being explored. A new transition probability model was then built for each set of altered capture histories using the structure of the top performing model as determined by QAICc ranking (i.e. the most parsimonious model built with the Scenario 1 input file).

We considered five different PA scenarios: the current MSDR boundary (Scenario 1), three scenarios with expanded boundaries (Scenarios 2–4), and one scenario with no PA (Scenario 5) (Fig. 3). Scenarios 2–4 represented an expansion in the boundaries that included segments of the Japurá River. In Scenario 2, an area of $4.968 km^2$ directly adjacent to the entrance of the MLS was included as protected (Fig. 3). Scenario 3 included the same area in Scenario 2 plus the area where the Japurá meets the Solimões River, totaling $7.024 km^2$ of additional protected water (Fig. 3). Scenario 4 included a total additional area of $16.633 km^2$, consisting of the area protected in Scenario 3 plus an additional large segment upriver (Fig. 3). Finally, to simulate a scenario with no reserve (Scenario 5), the apparent survival both inside and outside the MSDR was set equal to 0.834.

We expected that protecting sections of the Japurá would benefit the population because during LW, when botos are forced out of the MSDR, many individuals are seen near the MSDR entrance (Martin and da Silva, 2004a; Mintzer et al., 2016). If botos do indeed utilize this area of the Japurá extensively, we would expect transition probabilities going from inside to outside the MSDR to decrease considerably in scenarios where the PA boundary is expanded to include this area. Subsequently, we would expect abundance estimates to be greater for PA scenarios including the Japurá sections since some killing of botos is known to occur in this area (e.g., Mintzer et al., 2015). With a decrease in transition probabilities leaving the MSDR, botos would be subject to a lower mortality probability for longer periods of time.

3. Results

3.1. Model performance

The trend in abundance predicted by the evaluative model closely followed the trend expected with an annual 6.7% decline (Fig. A.1); thus, none of the original parameter estimates were adjusted. As expected, the modeled abundance of botos fluctuated in accordance with the season (Mintzer et al., 2016; Martin and da Silva, 2004a, 2004b). The lowest number of botos within the MSDR occurred during LW (Fig. A.2).

Table 1
QAICc table from multi-state models estimating transition probability (Ψ) of Amazon river dolphins moving in and out the Mamirauá Sustainable Development Reserve.

Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	k[a]
1. Ψ (CSeasonLG2)[b,c]	3360.98	0.00	0.69	62
2. Ψ (SeasonLG2)	3362.62	1.63	0.31	82
3. Ψ (CSeasonLG3)	3371.69	10.71	0.00	70
4. Ψ (CSeasonLG4)	3383.79	22.80	0.00	78
5. Ψ (SeasonLG3)	3390.88	29.89	0.00	100

[a] The number of estimated parameters (k) is listed for each model.
[b] The parameter of primary interest was transition probability (Ψ). Season-dependence (Season), state/location-dependence (L), and group effect (G) were represented with the associated symbols. Condensed season-dependence (CSeason) corresponds to models where estimation of transition probabilities was restricted per season across all years. Different group combinations were considered: adult males, adult females, mother/calf pairs, and immature individuals (G4); adults, mother/calf pairs, and immature individuals (G3); adults, and then mother/calf pairs and immature individuals combined (G2).
[c] Parameters Φ and p were fixed through *a priori* assumptions.

3.2. Transition probabilities

The median $\hat{c}$ goodness-of-fit test resulted in $\hat{c} = 2.223$, well within an acceptable range of $1 \leq c \leq 4$ (Burnham and Anderson, 2002), and all multi-state model results were adjusted with this value. QAICc supported a model with condensed season-dependent transition probabilities, and with two groups, adults (AM and AF), and MCI (MCP and IMM) (Model 1; Table 1; Fig. A.3). Thus, this model structure was used to build the additional multi-state models to estimate transition probabilities for the various scenarios. The difference in transition probabilities between adults and MCI was expected based on Mintzer et al. (2016).

The transition probabilities in the direction away from the MSDR (Ψ^{MA}) varied considerably with the adjustments made to the input files. As expected, these estimates decreased as the MSDR boundary was expanded to include the Japurá River in the various scenarios, particularly for the FW season. The largest estimated difference was between the transition probabilities of the adult group in the direction leaving the MSDR between Scenario 1 ($\Psi^{MA}_{Adults, LW} = 0.602$; SE = 0.057) and Scenario 4 ($\Psi^{MA}_{Adults, LW} = 0.326$; SE = 0.043) (Fig. A.3).

3.3. Scenario predictions

The abundance estimates corresponding to the current scenario (Scenario 1; Fig. 3) predicted a decline in the study population, with only 17 botos remaining after 50 years (Fig. 4). The estimates for Scenario 5, representing no PA status, predicted that in 30 years the population would decline to 7 individuals (Fig. 4). In Scenarios 2 and 3 (Fig. 3), where the PA boundaries were expanded to include small segments of the Japurá adjacent to the entrance of the MLS, the model predicted more gradual declines in abundance (Fig. 4). In Scenario 4, where the PA was expanded considerably to include a larger portion of the Japurá (Fig. 3), the model predicted a relatively small change in abundance in the next 50 years, with over 500 botos remaining (Fig. 4).

4. Discussion

4.1. Abundance trends

Da Silva et al. (2011), Mintzer et al. (2013), and da Silva et al. (2018b) showed that the killing of botos for use as bait is having a detrimental effect on the study population. It was not surprising that the model predicted a declining trend in the population under the current scenario (MSDR's true boundaries, Scenario 1). The model results suggested; however, that without any spatial protection (Scenario 5), boto abundance would decline at a faster rate. The results also showed that
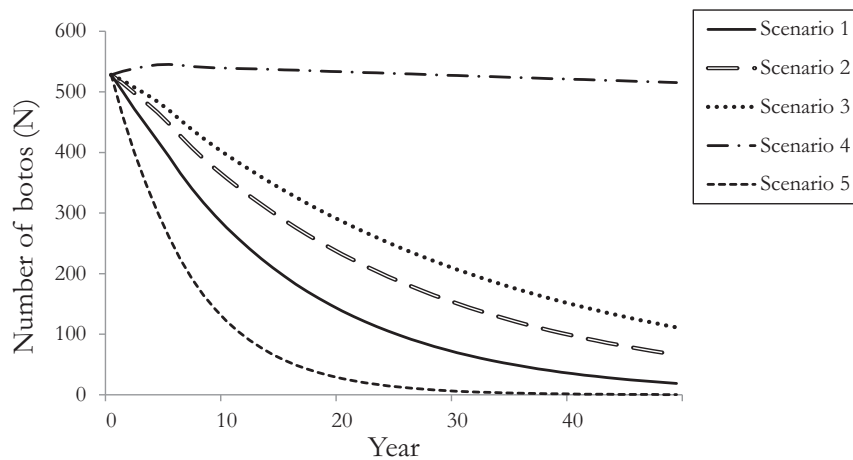
Fig. 4. Fifty-year abundance (N) trends of *Inia geoffrensis* estimated from five scenarios simulated in the evaluative population model. Scenario 1 represents the true or existing protected area boundary of the Mamirauá Sustainable Development Reserve. Scenarios 2–4 convey situations where the protected area boundary was expanded in the model. Scenario 5 represents the circumstances under no protected area.

Scenarios 2 and 3 would not result in substantial improvements to the population trend. Only Scenario 4 resulted in a relatively stable population.

4.2. Model limitations

The model assumed differences in survival between areas inside and outside the reserve, but homogeneity within those broad areas. Botos found outside the PA were subject to one mortality rate, regardless of their exact location. The same held true for botos found within the MSDR. Because there is no evidence that botos are purposely killed for bait within the segment of the MSDR included in this study (Mintzer et al., 2015), this assumption is reasonable for the inside state. On the other hand, hunting is not evenly distributed outside of the MSDR (Mintzer et al., 2015). Because we did not directly account for this heterogeneity, the trend in abundance as depicted in Scenario 4 could be an overestimation of boto abundance, as the survival probability could already be high in some areas outside the MSDR. However, the PA extension in Scenario 4 straddles a fishing community and the entrance of a channel where botos have been killed (Mintzer et al., 2015), so it is reasonable to assume that there would be an increase in survival probability in that area.

Both the transition probabilities and the evaluative model were structured according to the main hydroperiods. This structure, while adequate to represent the general exodus of botos from the MSDR, does not capture finer-scale movements (Mintzer et al., 2016). For example, some botos may leave the MSDR at high water and reenter at falling water before leaving again (Martin and da Silva, 2004a). In these cases, botos would be exposed to varying survival probabilities within the same week or day. A similar model based on weekly time intervals, would be highly data intensive, but could better depict these transitions (Mintzer et al., 2016).

4.3. Protected areas for Amazon River dolphins

The results of this study suggest that spatial protection can contribute to the conservation of boto populations that exhibit site fidelity to floodplains. However, at current hunting levels in the study area, solely protecting the flooded forest and its lakes will not be sufficient to maintain the study population, as individual botos are subject to high levels of mortality when leaving these areas. Given that the movement patterns of most individuals are predictable based on water level, and that many botos stay close to the *várzea* during low water, protecting areas of main rivers adjacent to *várzea* habitat, especially during low water, is essential. The model results suggest that these river PAs may need not be large relative to the floodplain PA (Scenario 4's PA expansion is equivalent to only 6% of the MLS), but need to include hotspots of boto activity outside the flooded forests such as confluences, channel entrances, and beaches, to assure that botos spend a considerable portion of their time within a PA.

The Japurá River, highlighted in our case study, is an important transportation route so expanding the MSDR boundary permanently to encompass the river (Scenario 4, Fig. 3) is likely not feasible. However, a protected area buffer zone could be implemented, where the MSDR enforcement would focus on limiting boto killing in this area without placing other PA restrictions (Mintzer et al., 2016). The buffer zone would need to be implemented primarily at low water when the highest proportion of the boto population is found outside the MSDR.

This study focused on a boto population that exhibits high site fidelity, with at least half the individuals considered residents (Martin and da Silva, 2004b). Not all botos exhibit a high degree of site fidelity and PAs may do little to protect transient individuals that may travel hundreds of kilometers between river systems (Martin and da Silva, 2004a). However, site fidelity to *várzeas* or lakes has also been observed in botos in the River Negro, Tocantins River, Samiria River, and Orinoco basin (Best and da Silva, 1989; Schnapp and Howroyd, 1992; McGuire and Henningsen, 2007), so spatial protection may be a beneficial strategy throughout the species' range. However, localized studies would need to identify fine-scale areas of preferred boto use throughout the year (i.e., encompass all hydroperiods), with special focus on identifying hot spots of boto activity during low water. When possible, these studies should include participation of human communities living in and near the existing or proposed PAs.

Throughout the Amazon, federal enforcement is challenging due to institutional deficiencies (Peres and Terborgh, 1995; Trujillo et al., 2010; Utreras et al., 2010); thus, PAs will likely not be successful in limiting boto killing without strong local efforts. We know, for example, that botos have been killed within the MSDR boundaries (Estupiñán et al., 2003; Iriarte and Marmontel, 2013a; Mintzer et al., 2015) where enforcement and management efforts are not carried out to the same degree as in the primary study area (the MLS and adjacent waterways) (SCM, 1996). The killing of botos has been limited in the MLS likely due to a combination of researcher presence, education resulting from boto research and the MSDR community-based programs, and the MSDR enforcement agent surveillance (Mintzer et al., 2015). Such a combination of programs in an Amazonian protected area is uncommon. Nevertheless, the management scheme implemented in the southern portion of the MSDR provides a concrete example of these types of

efforts and can serve as a guide for other sustainable use PAs (SCM, 1996; Mintzer et al., 2015). It is difficult to speculate on how PAs with other management schemes would perform in terms of maintaining local boto abundance. In theory, a strict nature reserve should provide full protection for wildlife. However, in cases with poor federal enforcement, the lack of local community participation in enforcement and research could be a hinderance to boto conservation.

From 2015 to 2019, the Brazilian government enacted a 5 yr moratorium on the *piracatinga* fishery (Interministerial Normative Instruction 6, of July 17, 2014). To date, there are no comprehensive studies or reports available that indicate how the ban was implemented and its effectiveness in decreasing *piracatinga* catch and exportation. *Piracatinga* continued to be fished throughout the Brazilian Amazon during the moratorium as evident by the identification of *piracatinga* in markets and freezing plants (da Silva et al., 2018c) and the seizing of illegal catch by federal enforcement throughout 2017–2019 (da Silva et al. Unpublished results). Gear utilized for fishing *piracatinga* (i.e., corrals and boxes) were still observed in the proximity of the MSDR in 2017–2019 suggesting that the fishery persisted near the reserve (Marmontel et al., 2020). However, anecdotal reports indicate that the killing of botos decreased in the region. Impending assessments on boto survival rates may provide insight on the effects of the ban, if any, on the Mamirauá boto population. Further modeling could incorporate updated survival rates to reevaluate the role of spatial protection within the context of a fishery moratorium.

4.4. Protected area evaluation

Because most PAs are monitored only after establishment, one of the main challenges in PA evaluation is a lack of pre-PA data that allows for pre- and post-PA comparisons. Evaluations are further complicated in cases were insufficient data exists to make comparisons between populations occurring inside and outside PAs. In this study, regardless of these challenges, a fairly simple population model was used to evaluate a PA and assess potential design improvements. The mark-recapture/resight data set used here allowed for key parameter estimates to inform the model, particularly survival probability estimates that represented protected vs. unprotected areas and transition probabilities that measured movement between these areas. If a mark-recapture/resight data set is available to estimate these demographic parameters, our framework could be used to evaluate PAs in other systems for other species.

CRediT authorship contribution statement

Vanessa Mintzer: Conceptualization, Methodology, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Reviewing & Editing, Visualization, Project Administration, Funding acquisition. **Vera da Silva:** Investigation, Resources, Data Curation, Writing – Reviewing & Editing, Project Administration, Funding acquisition. **Anthony Martin:** Investigation, Resources, Data Curation, Writing – Reviewing & Editing. **Thomas Frazer:** Conceptualization, Resources, Writing – Reviewing & Editing, Supervision. **Kai Lorenzen:** Conceptualization, Methodology, Formal Analysis, Resources, Writing – Reviewing & Editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary methods and figures

Transition probability modeling details, fifty-year abundance estimates compared with a 6.7% average annual decline (Fig. A.1), five-year model abundance estimates inside and outside the MSDR (Fig. A.2), and transition probability estimates for boto groups (Fig. A.3). Supplementary items to this article can be found online at doi:https://doi.org/10.1016/j.biocon.2020.108851.

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